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The current state of CO2 flux chamber studies in the Arctic tundra : A review

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2018-04

Virkkala , A-M , Virtanen , T , Lehtonen , A , Rinne , J & Luoto , M 2018 , ' The current state of CO2 flux chamber studies in the Arctic tundra : A review ' , Progress in Physical Geography , vol. 42 , no. 2 , pp. 162-184 . https://doi.org/10.1177/0309133317745784

http://hdl.handle.net/10138/307190
https://doi.org/10.1177/0309133317745784

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Progress in
Physical Geography

The current state of CO_2 flux chamber studies in the tundra: a review

Journal:	*Progress in Physical Geography*
Manuscript ID	PPG-17-050.R1
Manuscript Type:	Main Article
Keywords:	Arctic, chamber, ecosystem respiration, gross primary production, net ecosystem exchange, tundra

Abstract:	The Arctic tundra plays an important role in the carbon cycle as it stores 50 % of global soil organic carbon reservoirs. The processes (fluxes) regulating these stocks are predicted to change due to direct and indirect effects of climate change. Understanding the current and future carbon balance calls for a summary of the level of knowledge regarding chamber-derived CO_2 flux studies. Here, we describe progress from recently (2000-2016) published studies of growing-season CO_2 flux chamber measurements, namely GPP (gross primary production), ER (ecosystem respiration), and NEE (net ecosystem exchange), in the tundra region. We review the study areas and designs along with the explanatory environmental drivers used. Most of the studies were conducted in Alaska and Fennoscandia, and we stress the need for measuring fluxes in other tundra regions, particularly in more extreme climatic, productivity, and soil conditions. Soil respiration and other greenhouse gas measurements were seldom included in the studies. Although most of the environmental drivers of CO_2 fluxes have been relatively well investigated (such as the effect of vegetation type and soil microclimate on fluxes), soil nutrients, other greenhouse gases and disturbance regimes require more research as they define the future carbon balance. Particular attention should be paid to the effects of shrubification, geomorphology, and other disturbance effects such as fire events, and disease and herbivore outbreaks. An improved conceptual framework and understanding of underlying processes of biosphere-atmosphere CO_2 exchange will provide more information on carbon cycling in the tundra.

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Abstract

The Arctic tundra plays an important role in the carbon cycle as it stores 50 % of global soil organic carbon reservoirs. The processes (fluxes) regulating these stocks are predicted to change due to direct and indirect effects of climate change. Understanding the current and future carbon balance calls for a summary of the level of knowledge regarding chamber-derived CO_2 flux studies. Here, we describe progress from recently (2000-2016) published studies of growing-season CO_2 flux chamber measurements, namely GPP (gross primary production), ER (ecosystem respiration), and NEE (net ecosystem exchange), in the tundra region. We review the study areas and designs along with the explanatory environmental drivers used. Most of the studies were conducted in Alaska and Fennoscandia, and we stress the need for measuring fluxes in other tundra regions, particularly in more extreme climatic, productivity, and soil conditions. Soil respiration and other greenhouse gas measurements were seldom included in the studies. Although most of the environmental drivers of CO_2 fluxes have been relatively well investigated (such as the effect of vegetation type and soil microclimate on fluxes), soil nutrients, other greenhouse gases and disturbance regimes require more research as they might define the future carbon balance. Particular attention should be paid to the effects of shrubification, geomorphology, and other disturbance effects such as fire events, and disease and herbivore outbreaks. An improved conceptual framework and understanding of underlying processes of biosphere-atmosphere CO_2 exchange will provide more information on carbon cycling in the tundra.

Keywords

Arctic, tundra, chamber, net ecosystem exchange, gross primary production, ecosystem respiration

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I Introduction

Tundra regions are expected to experience stronger climate warming than other regions in the world (Hinzman et al., 2013; Stocker et al., 2013). They are also highly sensitive to environmental change, which may potentially alter their ecological dynamics (Hinzman et al., 2005; McGuire et al., 2009; Post et al., 2009). Higher air temperatures have already been observed to alter permafrost extent (Osterkamp and Romanovsky, 1999; Schuur et al., 2009), vegetation distribution (Elmendorf et al., 2012; Forbes et al., 2010; Hudson and Henry, 2009; Tape et al., 2006), and hydrological cycles (Mernild et al., 2012; Overeem and Syvitski, 2010; Smol and Douglas, 2007). These changes are tightly linked to the tundra carbon cycle which plays an important role in the global carbon balance: northern tundra regions store approximately 50 % of global soil organic carbon (SOC) stocks (Hugelius et al., 2014; McGuire et al., 2009; Tarnocai et al., 2009). Whether tundra regions will act as a carbon sink, or as a carbon source, in a warmer climate remains uncertain (Belshe et al., 2013; McGuire et al., 2012; Sitch et al., 2007).

The SOC stocks and the carbon balance are regulated mainly by CO_2 and CH_4 exchange between the biosphere and the atmosphere (McGuire et al., 2010a). Moreover, the lateral transport of organic and inorganic carbon in soil water transfers carbon to streams and rivers in a dissolved or particulate form (McGuire et al., 2010b; McGuire et al., 2009; Parmentier et al., 2017). Two processes, or fluxes, dominate the biosphere-atmosphere exchange: CO_2 uptake by ecosystems via photosynthesis (GPP: gross primary production), and carbon release to the atmosphere via plant and microbial respiratory losses (ER: ecosystem respiration) (Callaghan et al., 2004). The CO_2 balance between these two fluxes is called NEE (net ecosystem exchange).

Future climate warming can affect CO_2 fluxes in multiple ways (Arens et al., 2008; Biasi et al., 2008; Bokhorst et al., 2010). On the one hand, warming might accelerate soil respiration by heterotrophs, i.e. the microbial decomposition of organic matter, thus increasing respiratory carbon losses (Grogan and Chapin, 2000; Nadelhoffer et al., 1991). These emissions may be multiplied if permafrost soils thaw and the carbon stored therein will

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become available for decomposition (Kuhry et al., 2010; van Huissteden and Dolman, 2012). On the other hand, increases in temperature, greater release of available soil nutrients via accelerated decomposition, and a longer growing season have the potential to stimulate GPP and strengthen the carbon sink (Cahoon et al., 2012; Leffler et al., 2016). Changes in the CO_2 fluxes can therefore either increase or decrease NEE and thus create either a negative or positive feedback to global warming. A recent meta-analysis based on 54 studies suggested that there has been an increase in the CO_2 source due to higher ER, resulting in amplified carbon losses to the atmosphere in warmer conditions (Belshe et al., 2013).

Though climatically controlled, the magnitudes, directions, and feedbacks of GPP and ER are ecosystem- and scale-dependent (Oberbauer et al., 2007; Pare and Bedard-Haughn, 2012). Tundra landscape heterogeneity (Fletcher et al., 2012; Post et al., 2009; Virtanen and Ek, 2014) is apparent at multiple scales. At the landscape scale, diverse environmental conditions and vegetation types create mosaic of ecosystems, for example, bogs, and barrens. These ecosystems, in turn, are made up of diverse plant-communities, such as heaths, tussocks, or hummocks. At this fine scale, environmental conditions can change within only a few meters (Aalto et al., 2013). Such variation might offset climatological effects and buffer climate change -induced modifications in CO_2 fluxes (Post et al., 2009). For example, the environmental gradients of soil moisture are an important driver of CO_2 fluxes (Nobrega and Grogan, 2008; Oberbauer et al., 2007; Sharp et al., 2013). However, the fine-scale variation of CO_2 fluxes is not yet fully understood. This may hinder our ability to predict the future carbon balance.

GPP, ER, and NEE are studied with various methods in the field. There are two widely used techniques to measure CO_2 fluxes between ecosystems and the atmosphere: the micrometeorological eddy covariance (EC) technique, and chamber measurement techniques. EC measures fluxes continuously at an ecosystem scale in areas between 100 m^2 to 10 000 m^2, thus averaging over fine-scale heterogeneity (Kade et al., 2012; Maanavilja et al., 2011). However, using detailed land cover and wind direction information, flux sources can to some extent be estimated by footprint modelling techniques (Fox et al., 2008; Soegaard et al., 2000). Studies investigating individual plant communities and fine-scale spatial variability (100–10 000 cm^2) in the tundra are usually conducted using chambers. Both abovementioned methods have their limitations. The costs of setting up and maintaining an EC tower are higher than for the chamber method. Additionally, EC requires more electricity, technical knowledge, and understanding of surface-layer meteorology; whereas chambers are widely used due to low power consumption and simple operation. However, manual chamber measurements are laborious. With the

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chamber method, the different components of CO_2 exchange can be studied, thus providing important data on the processes regulating biosphere-atmosphere interactions (McGuire et al., 2012).

In order to understand CO_2 fluxes at multiple scales, reviews and meta-analyses are important to summarize the current knowledge. Comprehensive works exist on the Arctic carbon cycle as a whole (McGuire et al., 2009; Parmentier et al., 2017), on the vulnerability of permafrost carbon (Abbott et al., 2016; Ping et al., 2015; Schuur et al., 2008), and on the CO_2 and carbon balance of tundra regions during the past 20-40 years (Belshe et al., 2013; McGuire et al., 2010b, McGuire et al., 2012, Oechel et al., 1993, Oechel et al., 2000). Although these analyses include chamber studies, the main focus has been on the effects of large-scale drivers and temporal changes on CO_2 fluxes. To our knowledge, no previous reviews or meta-analyses focus on chamber studies of GPP, ER, and NEE with an emphasis on fine-scale vegetation and soil variables.

In this review, we synthesize the progress of chamber-derived growing season CO_2 flux studies in terrestrial Arctic tundra. We focus on chamber studies as they have been and will continue to be a central and cost-efficient method to study the underlying processes in CO_2 exchange, and are able to account for the fine-scale spatial variability of these processes. GPP and ER are the most important fluxes considered (Cahoon et al., 2012; Illeris et al., 2004), as they are processes that govern the net exchange of CO_2 between an ecosystem and the atmosphere. Furthermore, the balance of these two, NEE, is also incorporated in the review. We review the study areas and study designs where GPP, ER, and NEE are investigated and identify environmental conditions not sufficiently covered by these studies. Our aim is to examine the explanatory variables used and whether they correspond to mechanisms of known importance. Chapter 2 will give a short introduction to the tundra carbon cycle and chapters 3 to 6 encompass a systematic review of 93 articles found via ISI Web of Science (WoS) and subsequently from the references therein. We include recent publications only (studies published 2000 – 2016: Supplementary Material 1, S1) to determine the current state of CO_2 flux chamber studies in the tundra environment.

II Carbon cycle in a tundra environment

The spatial extent of Arctic tundra regions (from here on, tundra regions) can be defined in various ways. Here, we consider the tundra as a biome of treeless vegetation and their adjacent tree-line areas in the arctic and oro-arctic regions (as suggested by Virtanen et al.

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2016). Sub-Arctic and Arctic peatlands were included in the review whilst boreal regions were excluded as we concentrated on tundra patterns and processes only. Thus defined, tundra regions cover 8.7 % of global terrestrial areas (Dinerstein et al., 2017) and are characterized by low summer temperatures and long winters (Billings and Mooney, 1968).

Due to low solar energy input and harsh climatic seasonality, primary production, respiration, and decomposition rates are slow. Significant seasonal cycles in these processes exist largely due to snow cover and the short, two-to-four-month growing season (Leffler et al., 2016; van der Molen et al., 2007). Photosynthesis only occurs during the summer, whereas decomposition and respiration occur throughout the year, albeit at slower rates in winter (Larsen et al., 2007). The growing season is the most active season for GPP and ER, although spring and autumn CO_2 fluxes can contribute up to 19 % of annual GPP (Larsen et al. 2007). GPP and ER may fluctuate on inter-annual and longer time scales due to the variations in for example, climatic parameters. Diurnal cycles are also notable: daytime GPP usually offsets ER, but at night ER becomes dominant (López-Blanco et al., 2016). NEE, defined as NEE=ER-GPP, is usually a small difference between two large fluxes which makes it sensitive to small changes. Based on observations, tundra regions can be either carbon sources or sinks with large temporal variation on inter-annual and decadal scales (Lopez-Blanco et al., 2016). Typical NEE values are, for example, -79 - -41 g C m^{-2} yr^{-1} in a Russian erect shrub tundra - wetland complex (Marushchak et al., 2013), -4 g C m^{-2} yr^{-1} in a Fennoscandian fen (Aurela et al., 2004), and -2.3 g C m^{-2} yr^{-1} in an Arctic valley in Greenland (Soegaard et al., 2000), with negative values indicating a net carbon uptake by ecosystems. These estimates are smaller than for the neighboring boreal and temperate regions, but they have the potential to change in a warmer climate (Parker et al. 2015; Hartley et al. 2012).

Although tundra regions lack the trees that dominate carbon exchange in forested ecosystems, they have highly variable vegetation patterns. One of the most common ways to describe tundra vegetation is the Circumpolar Arctic Vegetation Map (CAVM; e.g. Pearson et al., 2013; Raynolds et al., 2008) created by Walker et al., (2005). They divide the Arctic based on the general appearance of vegetation into the following habitat-scale physiognomic categories and further into specific mapping units based on plant functional types (PFT's): barren (B), graminoid (G), prostrate-shrub (P), erect-shrub (S) and wetland (W) tundra, all of which have distinct CO_2 flux patterns (Figure 1). GPP usually exceeds ER, leading to a net uptake of carbon (negative NEE) during the growing season in all CAVM categories except in barren vegetation types. In general, deciduous shrubs and graminoids have the highest GPP due to high leaf area and vegetation cover, with graminoids having even larger ER due to their faster metabolism (Cahoon et al., 2012; Hobbie, 1996; Nobrega

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and Grogan, 2008; Oberbauer et al., 2007). Yet, the annual leaf development cycle of deciduous plants shortens their carbon uptake period in the early and late growing season. Evergreen shrubs and cryptograms, on the other hand, start photosynthesizing as soon as the ground is snow-free (Douma et al., 2007; Street et al., 2012).

III Study designs and locations

1 Overview of the studies

During the 21st century, most of the studies have focused on the effects of climate warming and related feedbacks on CO_2 fluxes (Biasi et al., 2008; Boelman et al., 2003; Welker et al., 2004), differences between vegetation types (Shaver et al., 2007; Williams et al., 2006), hydrological effects (Dagg and Lafleur, 2011; Nobrega and Grogan, 2008), and growing season dynamics (Bäckstrand et al., 2008; Larsen et al., 2007). The effect of permafrost thaw on CO_2 fluxes has not received a lot of attention until lately (Natali et al., 2011; Schuur et al., 2009b; Vogel et al., 2009). The most cited articles (>100 citations) within the literature reviewed focused on the effects of experimental warming and permafrost thaw on CO_2 fluxes and their spatial variation (S3).

The geographical distribution of observations in the CO_2 flux chamber studies is clustered in Alaska (32 out of 93 studies) and Fennoscandia (27), with smaller clusters scattered across Greenland (18), Russia (13), and northern Canada and Svalbard (8, Figure 2A). The observation sites do not cover the environmental variation, nor the extreme conditions, found in the Arctic (Figure 2B). Extreme conditions are generally found in the middle and eastern parts of Russia, and along coastlines and islands of northern Canada and Greenland. The environmental conditions in Alaska and Fennoscandia are characterized by relatively high precipitation, semi-oceanic climates, and acidic or mildly acidic soil conditions. In addition to these spatial limitations, continuous sampling of CO_2 fluxes remains a challenge (McGuire et al., 2012). While there are many studies with measurements from multiple growing seasons (Arens et al., 2008; Olivas et al., 2010), there are not many year-round observations (S4). The cold season (autumn, winter and spring) has been included in some studies, mainly in order to understand the role of non-growing season vs. growing season CO_2 fluxes and their drivers (Grogan and Jonasson, 2005; Kade et al., 2012; Larsen et al., 2007).

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CO_2 flux chamber studies are usually based on relatively small data sets (median number of sites studied four). With small data sets, all environmental gradients (e.g. topography, radiation, hydrology, productivity) are difficult to cover. Often, studies are designed to simplify and understand the variation with the help of different classifications mainly based on vegetation (Christensen et al., 2000 on Cassiope, hummock, continuous fen, grassland and *Salix arctica*), soil moisture (Welker et al., 2000 on dry and wet), or a combination of these two (Dagg and Lafleur, 2010 on dry birch, mesic birch, dry tussock, wet tussock, dry heath, mesic heath, wet sedge). The topographic gradient has been considered mostly in the peatland studies with microtopographically varying hummocks and hollows (e.g. Poyatos et al., 2014), though there are some coarser scale topo-sequence studies (Williams et al., 2006).

Based on our findings, future research should focus more on extreme conditions. Areas of high precipitation and low temperatures (e.g. southeastern parts of Greenland) or high temperatures (e.g. southern Alaska) should also receive further attention. Additionally, neutral conditions (topsoil pH>6, e.g. along the coastlines of Nunavut and Siberia) and higher elevations (e.g. in eastern Siberia) need to be considered. Relatively large SOC stocks are found in the Northwestern or Yukon Territories in Canada, which have not received much consideration. As fluxes in Alaska and Fennoscandia are the most studied and cited, it seems that our understanding of CO_2 fluxes is limited to these regions and important knowledge regarding for example High-Arctic environments has not been adequately considered. We realize that logistical and infrastructural reasons are, to some extent, responsible for this pattern, but this may potentially lead to misinterpretations of the CO_2 exchange of the whole tundra region. Moreover, studies in calcareous regions are needed as the higher availability of nutrients in neutral areas may cause CO_2 fluxes to vary more than in acidic landscapes with low nutrient availability (Williams et al., 2006). Furthermore, we emphasize the need for better observational studies to understand the spatio-temporal variation of CO_2 fluxes along environmental gradients as the drivers and dynamics might change due to global warming (Shaver, et al., 2013; Zamolodchikov, 2015). We encourage future studies to measure CO_2 fluxes from various topographical conditions from fine, 1–10 m (Scherrer and Körner, 2011), to ecosystem and landscape scales, 10–1000 m (Billings, 1973), as the response of biota to climate warming varies depending on topographic position.

2 CO_2 flux chamber measurement methods

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Various chamber systems have been used for studying CO_2 fluxes. Most of the tundra CO_2 flux studies were conducted with manual chambers (82 studies) while automated systems are still rare (11) because of the high costs and infrastructure challenges (S4; e.g. Griffis et al., 2000; López-Blanco et al., 2016; Natali et al., 2011; Poyatos et al., 2014).

Chamber size plays an important role when studying CO_2 fluxes. Tundra regions are microtopographically heterogeneous and, therefore, smaller chambers (<30 cm in diameter) are more practical. However, with a larger chamber, the erroneous influence of chamber edges on measurements decreases. Based on our literature survey, chamber sizes (when measured from edges or diameter of the chamber) and heights vary from 15 to 100 cm. The average height is relatively low, limiting the vegetation type studied (S4). Regardless of chamber type and size, the air-proof sealing of the chamber into the ground is an important step when measuring fluxes (Hutchinson and Livingston, 2001). Traditionally, plastic or aluminium collars are put into the ground (depth 2-10 cm) and chamber placed atop of them. Collars are positioned into the ground just minutes, days (Dagg and Lafleur, 2011; Stewart et al., 2013) or weeks before the measurement (Nykanen et al. 2003; Heikkinen et al. 2002), or in the preceding year (Grogan and Jonasson, 2005). However, placing the collars into rocky soils or soils with long horizontal aboveground shoots and roots typical to some tundra plants (e.g. *Empetrum hermaphroditum, Dryas* sp.) without cutting them is a challenge. A method that uses the combination of a plastic skirt and metal chains instead of, or in addition to, collars has been developed and is widely used in the studies (Street et al., 2012; Street et al., 2007).

We stress the need for long-term measurements of CO_2 fluxes with automated chambers, as they provide important information about local carbon cycle dynamics and episodic events in the Arctic. Moreover, we recommend researchers to carefully consider the chamber size used, and the timing and placement of the collar into the ground. Measurement devices and calculation techniques also have an impact on the measured fluxes. For example, CO_2 fluxes may be underestimated when using linear regression as compared to nonlinear methods (Kutzbach et al., 2007).

3 Studied fluxes

From the global carbon balance perspective, NEE is an important flux variable to study as it describes whether the environment is acting as a CO_2 sink or source (Belshe et al., 2013). Yet, NEE itself is not a process but a balance between two simultaneous processes, GPP and ER, that are more strongly linked to environmental drivers. Although studying NEE is crucial, many articles state that the future carbon balance is regulated by ER (Cahoon et al., 2012; Biasi et al., 2008) or soil respiration (Knowles et al., 2016; Luo et al., 2016). Despite this, soil respiration was measured in relatively few studies (15) together with GPP, ER, and NEE. Moreover, CO_2 fluxes are linked to other biogeochemical (N_2O, CH_4 and H_2O) fluxes. Methane (CH_4) fluxes were studied in 24 studies, out of which most of the measurements were from wetlands (S4). Other fluxes, such as nitrous oxide (N_2O; e.g. Brummell et al., 2012; Kelsey et al., 2016) or water (H_2O; e.g. Douma et al., 2007) were studied even less in CO_2 flux chamber studies, partly because according to current knowledge, N_2O emissions are significant in only non-vegetated patches with high soil organic matter content (Marushchak et al., 2011). They are increasingly measured alone (Flessa et al., 2008; Gil et al., 2017; Voigt et al., 2017), without CO_2 exchange measurements. Chamber-derived CO_2 fluxes have also been investigated together with EC and leaf cuvette methods (Heikkinen et al. 2002; Vourlitis et al. 2000). Studies with EC aimed to 1) describe the annual variation of CO_2 fluxes more reliably, and 2) test the upscaling potential of chambers for EC measurements with varying success in summer- and wintertime (Kade et al., 2012; Maanavilja et al., 2011; Marushchak et al., 2013). In total, EC was used in 11 studies and leaf cuvette measurements 5 (S4).

Based on our findings, we suggest that future studies should incorporate soil respiration measurements into CO_2 flux chamber studies. However, there is no standard way of measuring soil respiration and most of the methods cause disturbance to the ground, or require laboratory work (Kuzyakov, 2005). Clipping the vegetation was a widely-used method in the investigated articles (Illeris et al., 2004; Nobrega and Grogan, 2008). In some articles, soil respiration was quantified from an non-vegetated soil close to other CO_2 flux measurements (Arens et al., 2008) or with incubation methods (Ylänne et al., 2015). Despite the disturbance caused by clipping, this might be a cost-efficient method for soil respiration measurements, providing there is a sufficient waiting period between the clipping and the measurements (Illeris et al., 2004). Incubation methods will provide robust information on the soil CO_2 emissions for more precise analyses. In addition to soil respiration measurements, the inclusion of non-CO_2 greenhouse gas measurements would provide better understanding of climate forcing, especially in wet regions (CH_4) and non-vegetated areas (N_2O) (e.g. Brummell et al., 2012) Furthermore, the incorporation of multiple flux measurement methods will provide more reliable and increasingly detailed information on the spatial and temporal variation of CO_2 fluxes (Myklebust et al., 2008).

IV Environmental drivers studied to explain fluxes

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GPP, ER and NEE are affected by multiple variables which can be divided into four categories: 1) biota, where the processes occur, 2) resources which are consumed by the biota, 3) regulators which affect the metabolic processes, and 4) disturbance which often destroys the biota and therefore influences the fluxes (Figure 1, 3). Here, we review how these four categories and their variable classes have been included in studies (Table 1). The environmental drivers used to explain fluxes varies depending on the research questions and study designs, yet we assume that with a systematic review (S2) of the environmental drivers measured in the studies, we can highlight overall research gaps.

1 Climate

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Air temperature and solar radiation are the most important climatic variables explaining CO_2 fluxes, both spatially and temporally, as temperature controls the metabolic activity of biologic organisms and energy from the sun drives photosynthesis (Lopez-Blanco, et al. 2016, see also Figure 1). Air temperatures and photosynthetically active radiation (PAR, or photon flux density PPFD) in the chamber and/or in the vicinity of loggers are almost always included in the studies, and are often used in the models explaining GPP, ER, and NEE (Karelin et al., 2013; Shaver et al., 2013; Williams et al., 2006).

CO_2 fluxes are driven by soil microclimate which varies spatially over short distances. Soil temperature does not have a direct effect on GPP but it is an important driver of ER (Larsen et al., 2007) as it stimulates soil respiration and decomposition (Grogan and Chapin, 2000). Soil moisture has been identified as a limiting factor for GPP (Nobrega and Grogan, 2008) and for soil and plant respiration, especially at the soil moisture extremes (Dagg and Lafleur, 2011; Giblin et al., 1991; Illeris et al., 2003). The importance of soil microclimate has been recognized in the studies: the temporally varying soil temperature, active layer depth (or thaw depth), soil moisture, and water table height are included in approximately 80 % of the studies (Figure 4). Soil temperature is also often used when modeling ER and NEE, sometimes together with other soil microclimatological variables such as active layer depth or water table height (Christensen et al., 2000; Segal and Sullivan, 2014). Water table height is an important variable, especially in the peatlands, as it controls the anoxic conditions needed for CH_4 emissions.

2 Vegetation

Vegetation plays an important role in controlling the variation of CO_2 fluxes as GPP and, partly, ER are processes occurring within the plant (Johnson et al., 2000). The reviewed studies always provide some information on the dominant species with varying degrees of additional data on vegetation properties (e.g. biomass, LAI). We collected data on the dominant and secondary species in each measurement plot from the articles and further divided it into CAVM categories (S2, S5). In many of the studies different measurement sites within the study area belonged to several CAVM categories.

Most of the research has been conducted for the most dominant vegetation types and species in the Arctic: on graminoid-dominated meadows (with species *Carex* sp., *Eriophorum* sp. in >20 of the studies) and prostrate shrub and erect shrub heaths (with species *Betula nana, Empetrum* sp., *Vaccinium vitis-idaea, V. uliginosum* in approximately 10-30 of the studies Figure 5A, S5). Fewer studies included cushion plants, forbs, or mosses and lichens (despite some observations from *Cassiope* sp., *Potentilla* sp., *Sphagnum* sp., *Dicranum* sp., *Cladonia* sp., Figure 5B, S5). There are relatively large differences among measured vegetation types in the most researched areas (Figure 5C). Despite the important role of *Betula nana*, taller low-shrubs such as *Salix* sp. and in some regions *Juniperus communis* and *Alnus* sp. species are also crucial in the shrubification of the Arctic, yet they were included in only a small amount of studies. Indeed, based on article keywords, very few studies aimed to study the effects of shrubification on CO_2 fluxes (Cahoon et al., 2016; Cahoon et al., 2012). Barren vegetation types, which cover 25 % of the region, are only included in less than 10 % of the studies, but have received more attention in Antarctica (Thomazini et al., 2016; Zhu et al., 2014).

Although *Eriophorum, Carex,* or *Betula nana* -dominated vegetation types have been relatively well studied they need to be investigated more thoroughly in different environmental conditions as CO_2 flux observations of tundra shrubs and sedges, together with moist meadows by streams, contain the largest and most varying CO_2 fluxes (Williams et al., 2006). Additionally, these are also key sites for CH_4 dynamics. Moreover, we stress the need for studies focusing on shrubification effects with a diverse combination of taller low-shrub species. In the CAVM region, low-shrub tundra can be found from European Russia, northwestern Siberia, and the Yukon-Kuskokwim River delta, as well as in southwestern parts of Greenland and locally along rivers and tree lines. Regionally, more observations are needed from wetlands in Alaska and prostrate shrubs in Siberia (4B). Although having only low CO_2 flux rates, we highlight the need for more studies in barren soils as these are underrepresented and their spatial coverage might increase resulting from melting glaciers (Mernild et al., 2012).

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In addition to plant functional types and plant species, other data on vegetation have been used to understand CO_2 fluxes in different environments (Cornelissen et al., 2003). Plants use carbon for growth and, therefore, plant biomass can be measured to understand carbon sequestration and allocation patterns (mass-ratio hypothesis; Grime, 1998). In addition to biomass measurements, LAI and NDVI have been used to link the amount of photosynthesizing leaves to carbon use patterns, out of which LAI has often been found to be the best predictor of CO_2 dynamics (Marushchak et al., 2013; Shaver et al., 2007; Street et al., 2007). NDVI and LAI measurements were included in approximately 25 studies and biomass sampling in 4 (S4). Plant traits (leaf N, vegetation height, see Dorrepaal 2007) were studied less than biomass (Figure 4), although the relationship between leaf N and CO_2 fluxes has received increasing attention (Street et al., 2012).

Based on our findings, we firstly highlight the need for more detailed analysis of vegetation properties and CO_2 fluxes. For example, the relationship between plant traits or growth and CO_2 fluxes remains uncertain (De Deyn et al., 2008). Additionally, there is a need to study the linkages of ER and biomass, as higher biomass is linked to higher GPP but not as clearly as to ER (Boelman et al., 2003; Douma et al., 2007; Poyatos et al., 2014). Lastly, we stress the need for vegetation data -based upscaling, particularly to landscape scales, which remains a challenge in carbon cycle studies (O'Rourke et al., 2015). Although chamber-derived GPP, ER, and NEE have linked to field-observations of spectral properties of vegetation and LAI (Boelman et al., 2003; Williams et al., 2006), this relationship has seldom been used to upscale results to larger areas with aerial or satellite imagery (Marushchak et al., 2013). More research of CO_2 fluxes and remote sensing -based indices at multiple resolutions (e.g. WorldView, Landsat, MODIS, see e.g. Curasi et al., 2016) is called for to develop the upscaling methodology. Recent progress of unmanned aerial vehicles (UAVs) offers CO_2 flux researchers new opportunities for fine spatial and hyperspectral resolution imagery data (Anderson and Gaston, 2013).To our knowledge, there are no published studies utilizing UAVs for CO_2 flux chamber measurements in the tundra.

3 Soils

GPP, ER and NEE are regulated by soil physical, chemical, and biological properties which vary greatly over short distances (Arnesen et al., 2007; Wang et al., 2010). Soil physical properties, particularly soil type, texture, and organic layer depth influence overall soil conditions (Buchmann, 2000; Grand et al., 2016) and are connected to soil temperature, depth of the active layer, and vegetation properties. Soil nutrients are an important

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resource for plants and soil microbes, therefore affecting GPP and ER (Grogan and Jonasson, 2005). Soil N together with P limit tundra productivity, leading to increases in GPP if nutrients are added to the soil (Arens et al., 2008; Shaver et al., 1998). Soil microbes (heterotrophic respiration) control soil respiration together with plant roots (autotrophic respiration) and, therefore, partly ER (Segal and Sullivan, 2014). Soil data is included in fewer studies than climate and vegetation data: soil type descriptions are included in 15 studies, litter biomass estimates in 7 studies, soil nitrogen data in 18, and SOC measurements in 15 of the studies (S4). Data from the soil microbes is included in eight studies.

We recommend future studies to at least describe the soil type (Jones et al., 2010) and organic layer depth to provide information on soil physical and chemical conditions (see e.g. Biasi et al., 2008). The inclusion of soil data is needed in spatial study designs as soil properties vary especially spatially. We highlight the need for better understanding of CO_2 flux – nutrient and SOC relationships (Williams et al., 2006) as recent studies have discovered the respiratory losses and carbon sequestration to soils to depend on soil geochemistry (Doetterl et al., 2015). Thus, including soil nutrient data, of for example N and P, also increases knowledge of the linkages between different biogeochemical cycles in the Arctic. We stress the need for easily measurable indicators of soil quality (e.g. soil pH, the color or depth of organic matter, e.g. White et al., 2004). Microbial activity should receive more attention as it is not yet fully understood how microbial communities and their functioning regulate ER and NEE and how they will respond to environmental change (Biasi et al., 2008; Hultman et al., 2015; Xue et al., 2016).

4 Disturbance

Geomorphological processes create disturbance that leads to heterogeneous abiotic and biotic conditions (le Roux and Luoto, 2014) potentially shaping CO_2 fluxes (Vogel et al., 2009). There is a small but increasing amount of publications that focus on the effect of fluvial processes (Curasi et al., 2016; Oberbauer et al., 2007), cryoturbation as in e.g. patterned ground and hummocks (Heikkinen et al., 2002; Maanavilja et al., 2011), and permafrost as in e.g. palsa mires (Bäckstrand et al., 2010; Nykanen et al., 2003) on CO_2 fluxes. Most of these studies have been conducted in northern Fennoscandia, though there is an increasing number of studies of permafrost thaw from Alaska (Natali et al., 2011; Schuur et al., 2009).

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CO_2 fluxes are mediated by biological disturbance (Falk et al., 2015; Sjögersten et al., 2011; Susiluoto et al., 2008). The tundra is grazed by large and small herbivores which can alter species composition, above- and belowground biomass and litter quality and, therefore, CO_2 fluxes (Cahoon et al., 2012; Metcalfe and Olofsson, 2015; Ylanne et al., 2015). Herbivory was included in 13 studies with a focus on larger herbivores such as reindeer and muskoxen (S4). Larval outbreak was included in one study (but see a new study by Lund et al., 2017). In addition to herbivory, disease outbreaks (plant pathogens) can modify CO_2 fluxes but they have only been studied to a rather limited extent in one study. Olofsson et al., (2011) demonstrated GPP to decrease during the growing season due to an outbreak of a parasitic fungus, *Arwidssonia empetri* in northern Sweden. Presently, intensive insect outbreaks are rare in the tundra, but this might change if the climate warms (Abbot et al., 2016).

Fire is an important disturbance in boreal regions, but has had only minor effects on tundra carbon cycling since the early Holocene (Kasischke and Turetsky, 2006). However, models predict an increasing amount of tundra fires in a warmer climate which has already been observed in Alaska (Hu et al., 2010; Krawchuk et al., 2009), but still the effect of fire disturbance on tundra carbon cycling has received relatively little attention. Although there are studies considering the SOC stocks before and after a fire (Bret-Harte et al., 2013; Mack et al., 2011), there are no CO_2 flux chamber studies related to fire in the tundra (but see e.g. Köster et al., 2016 on boreal regions).

The disturbance regime of the studied region is often well described in the study site description (e.g. Vourltilis et al., 2000), but it should be better incorporated into analyses due to predicted changes in occurrence in a warmer climate (Aalto et al., 2014; Koven et al., 2011). Moreover, we need more comprehensive analysis of the effect of disturbance in different conditions (e.g. in nutrient-rich vs. nutrient-poor environments, or high vs. low-Arctic) as the response of an ecosystem to e.g. drought, increased herbivory or fire differs depending on the location.

V Towards a conceptual framework

Conceptual frameworks to explain and describe the drivers and mechanisms of fine-scale spatio-temporal variation of CO_2 fluxes are lacking (Bardgett and Wardle, 2010; Callaghan et al., 2004; Xue et al., 2016). Tundra ecosystems are complex and heterogeneous, so to be able to predict future changes, we first need to create a good understanding on the current processes and variables affecting CO_2 fluxes. Firstly, we highlight the need for

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theoretical, analytical, and process-based justification for the choice of measured variables. Secondly, we stress the importance of understanding the direct and indirect relationships among the variables (for example, the importance of topography, Figure 3). Most of the reviewed publications include data on biota (vegetation), resources (radiation, soil moisture), and regulators (air and/or soil temperature) as these variables vary greatly both spatially and temporally (S4). Out of these drivers, air temperature, PAR, vegetation type, LAI and, occasionally, soil temperature and moisture and NDVI were the most important factors affecting CO_2 fluxes. Other environmental variables measured depend on the study location and design, and research questions. Measuring disturbance is challenging as disturbance often occurs as episodic events. Still, we encourage the investigators to describe the disturbance regime of the plot by for example collecting herbivory data or describing the active geomorphological processes.

1 Standardized methodology for site description of chamber studies

The description of the measured sites varies between the studies. Both species-level as well as plant functional type (PFT) descriptions are used in the literature. For example, classifications of meadow-heath (Oberbauer et al., 2007) and more precise groups based on the dominant species i.e. *Betula nana* and *Dryas octopetala* (Shaver et al., 2007) have been used in the studies. Because of the importance of vegetation in the carbon cycle, standardized and easily comparable descriptive information on vegetation is crucial in order to understand CO_2 fluxes. Although the vegetation data given by CO_2 flux researchers is descriptive, we encourage the investigators to use widely used plant community classifications in addition to their own. A comprehensive system for the grouping of plants with similar links to environmental conditions can reduce the complexity of the systems (Otieno et al., 2009). Here, we used CAVM (Walker et al., 2005) which was developed for biogeographic and landscape-scale purposes. It has been successfully applied to the carbon cycle studies and allows researchers to easily compare results (Arndal et al., 2009; Biasi et al., 2008; Douma et al., 2007). An even more precise hierarchical floristic classification system than CAVM which is based on a smaller habitat-scale has been developed by Mucina et al. (2016), but is currently available only for Europe. In addition, the Arctic Vegetation Archive (AVA) aims to combine Arctic vegetation data at plot-scale but is still under progress (Walker et al., 2016).

Despite a common grouping system and characteristic vegetation types, smaller wet patches, stream channels and transitional zones are equally important in the patchy tundra vegetation. Fletcher et al. (2012) have shown that the most abundant vegetation types (e.g.

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Betula nana or *Empetrum* heath) have a higher GPP than their mixed vegetation types (e.g. *Betula-Empetrum* heath). Therefore, measuring also less abundant transition zones and providing species cover data on the dominant and secondary species to locate them is important**.** Currently, species cover data is included in approximately only 50 % of the studies, and cryptogram (mosses and lichens) data in even less. Cryptograms cover large areas in the Arctic, and the crucial role of mosses in the carbon cycle has been identified, especially during spring when leaves of deciduous vascular plants are not yet fully developed but mosses are already photosynthesizing (Douma et al., 2007). Cryptogram quantification using remote sensing, and LAI determination, are much less studied as they are methodologically even more challenging than vascular plants. However, high-resolution satellite and UAV imagery might provide tools for robust vegetation characterization in the future (Fraser et al., 2016). In addition to standardized vegetation characterization, chamber researchers need a common platform, similar to Fluxnet created for EC studies (Baldocchi et al., 2001; Chu et al., 2017), to share data and develop methods and guidelines.

VI Summary and future research needs

Environmental variation can affect tundra CO_2 fluxes in multiple ways. These effects are not yet fully understood due to limitations posed by study locations, designs and environmental variables measured to explain chamber-derived CO_2 fluxes (Table 2). Even though study locations cover the environmental variation relatively well, more research is needed in extreme conditions (such as high precipitation and low temperatures, high topsoil pH, high SOC stock conditions). Study designs should focus on covering spatial variation in environmental conditions, vegetation and soils, within and between study areas. Additionally, both ends of the productivity gradient (low-shrubs and barren vegetation types) should be studied more thoroughly.

Ecologically and physically relevant variables have been included in the reviewed studies to varying degrees and some topics require new research more urgently than others. Chamber-derived CO_2 fluxes should be explained not only by microclimate and vegetation type, but also by other fluxes, soil microbes and nutrient availability, and disturbance data, to better understand ecosystem functioning. As tundra regions are typically nutrient-limited thus responding strongly to changes in nutrient availability, more studies on the relationship of soil nutrients and microbes with GPP, ER, and NEE measurements are urgently needed. Simultaneous measurements of other greenhouse gases and soil respiration together with CO_2 fluxes are particularly urgent themes as changes therein might be crucial in determining the future carbon balance.

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Finally, studies of CO_2 fluxes should focus on the sensitive processes – along with their transitions and thresholds in the ecosystem – that have the potential to change the carbon balance. According to an expert assessment of the most important processes in the changing Arctic environment (Abbott, et al. 2016), these sensitive processes include vegetation shifts, permafrost thaw as well as hydrological changes. The effect of permafrost thaw has received increasing attention, but it is still unclear how other geomorphological disturbance, fire events, shrubification, or disease and herbivory outbreaks influence CO_2 fluxes and the tundra carbon balance. It is thus crucial to deepen the understanding of these processes. A better conceptual framework and understanding of CO_2 fluxes will provide more information on the carbon cycling in the tundra.

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Figure 1. CO_2 fluxes are regulated by biota, resources, regulators, and disturbance, and vary depending on CAVM (Circumpolar Arctic Vegetation Map) categories resulting in different carbon balances. CAVM represents only the major vegetation units and is developed for landscape or circumpolar scales, although in reality most tundra landscapes are mosaics of several of these types and their subtypes (Walker et al., 2016). The GPP (gross primary production) and ER (ecosystem respiration) bars represent their rates: the darker the shade, the faster the process. Increased GPP is often linked to higher plant respiration rates and, therefore, increased ER (Johnson et al., 2000). Increased GPP also stimulates the rate of litter production, resulting in higher heterotrophic respiration rates (Boelman et al., 2003).

Figure 2. A) The spatial distribution of the observations in the study with a base map of soil organic carbon content. B) The environmental conditions of the observations (in black) versus the environmental conditions in the Arctic tundra (in grey). The data acquired from WorldClimv2 (1970-2000), Soilgrid (topsoil pH), NCSCDv2 (soil organic carbon, SOC), TERRA/MODIS NDVI -product (July, 2015), and GTOPO DEM (elevation) (see S1). The arctic area was defined by Ecoregions (Dinerstein et al., 2017). See S2 for more details.

Figure 3. The hierarchy and relationships of the environmental drivers regulating GPP (gross primary production), ER (ecosystem respiration) and NEE (net ecosystem exchange) from large to fine scale. The arrows represent the main direction of the effect, and the colors of the arrows have no meaning. The resource variables have mostly a direct link to GPP and ER, but regulators and disturbance affect the biota, and thus, GPP and ER.

Figure 4. Number and proportion of studies in which each environmental class was used. Climatological variables and biomass were studied the most, whereas other vegetation properties, soils, and disturbance the least.

Figure 5. A) Number and proportion of studies with observations from different CAVM (Circumpolar Arctic Vegetation Map) categories in the Arctic tundra. B) Number and proportion of studies with observations from the most dominant genera. C) Number and proportion of studies with observations from different CAVM categories per most intensively studied regions. The vegetation data is based on the dominant and secondary species informed by the authors, which was then used to classify the vegetation into CAVM categories. Note the differing proportions on the y-axis.

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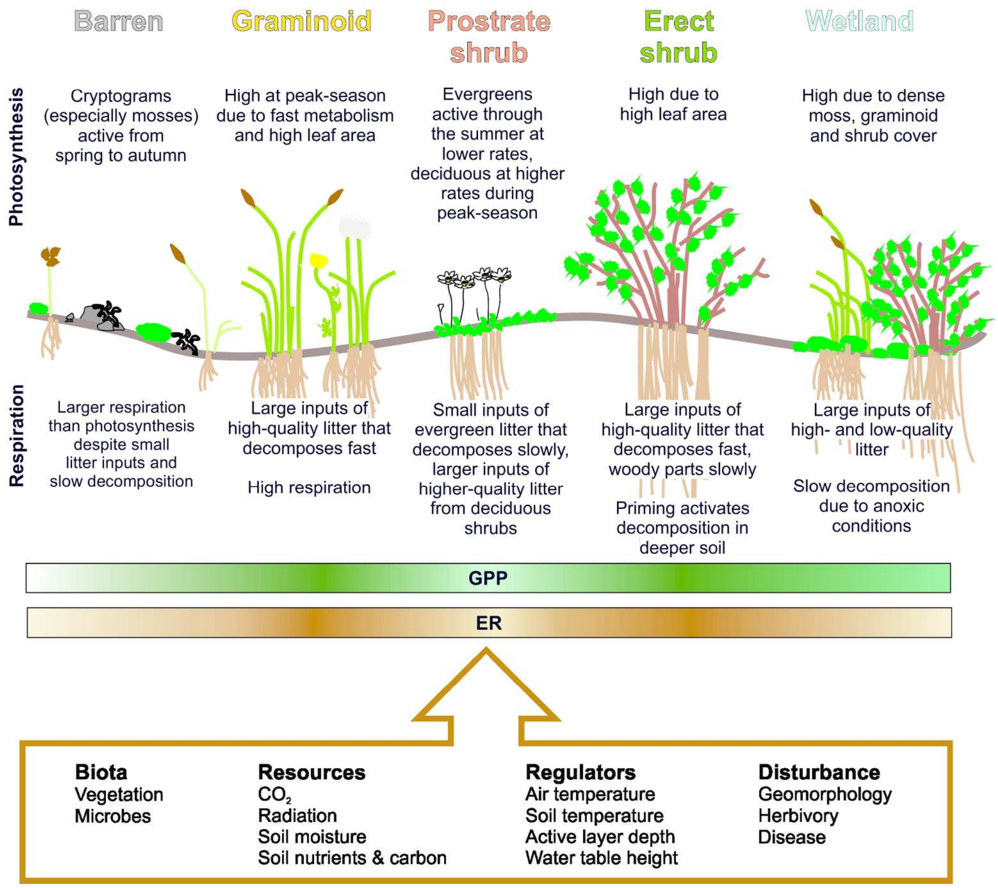

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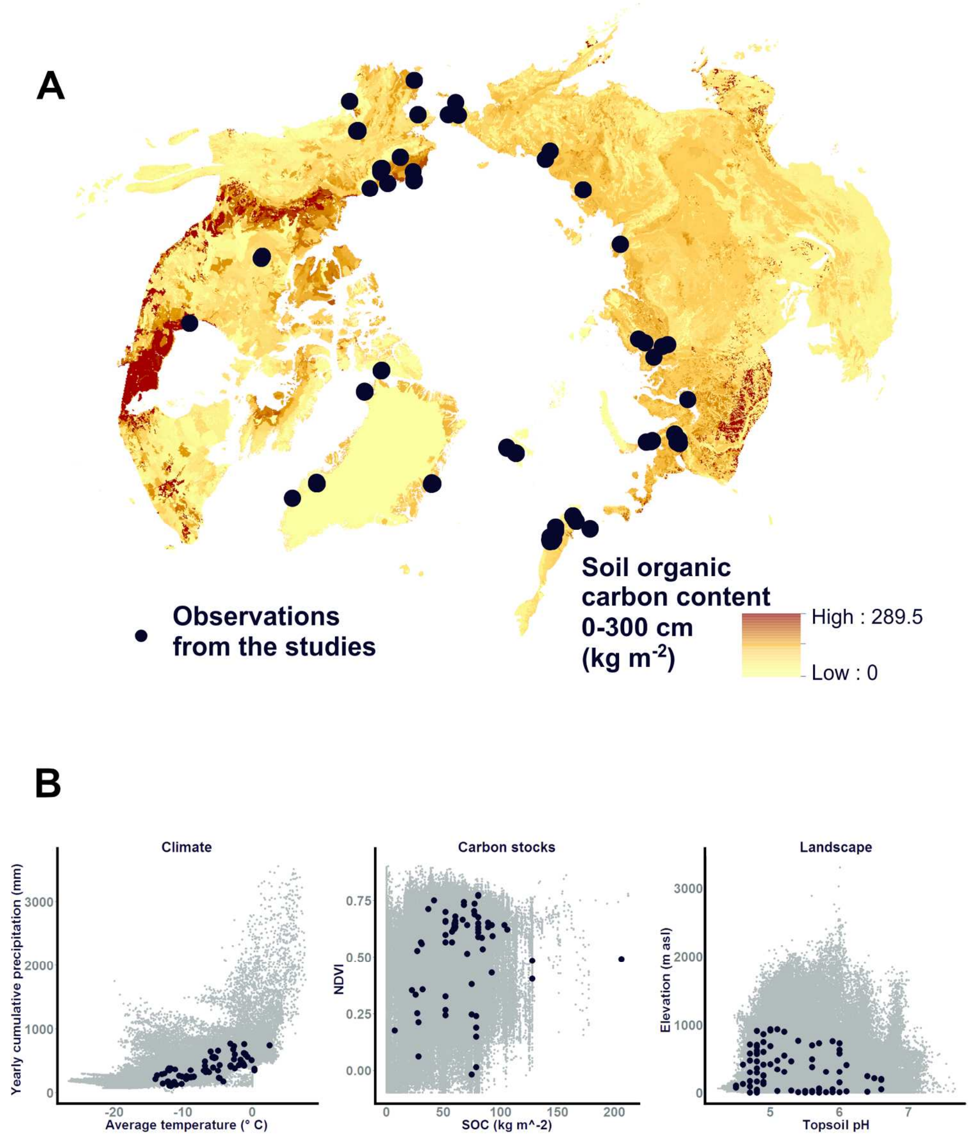

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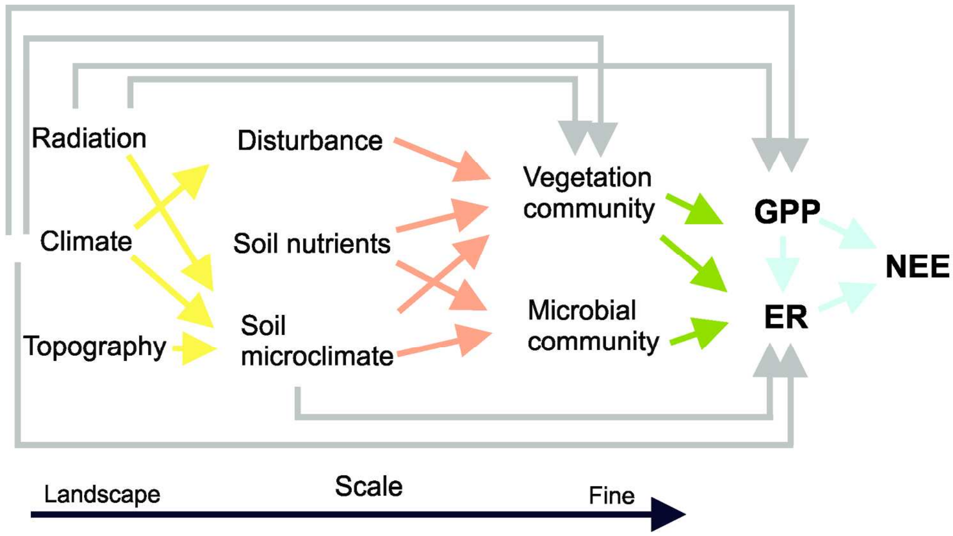

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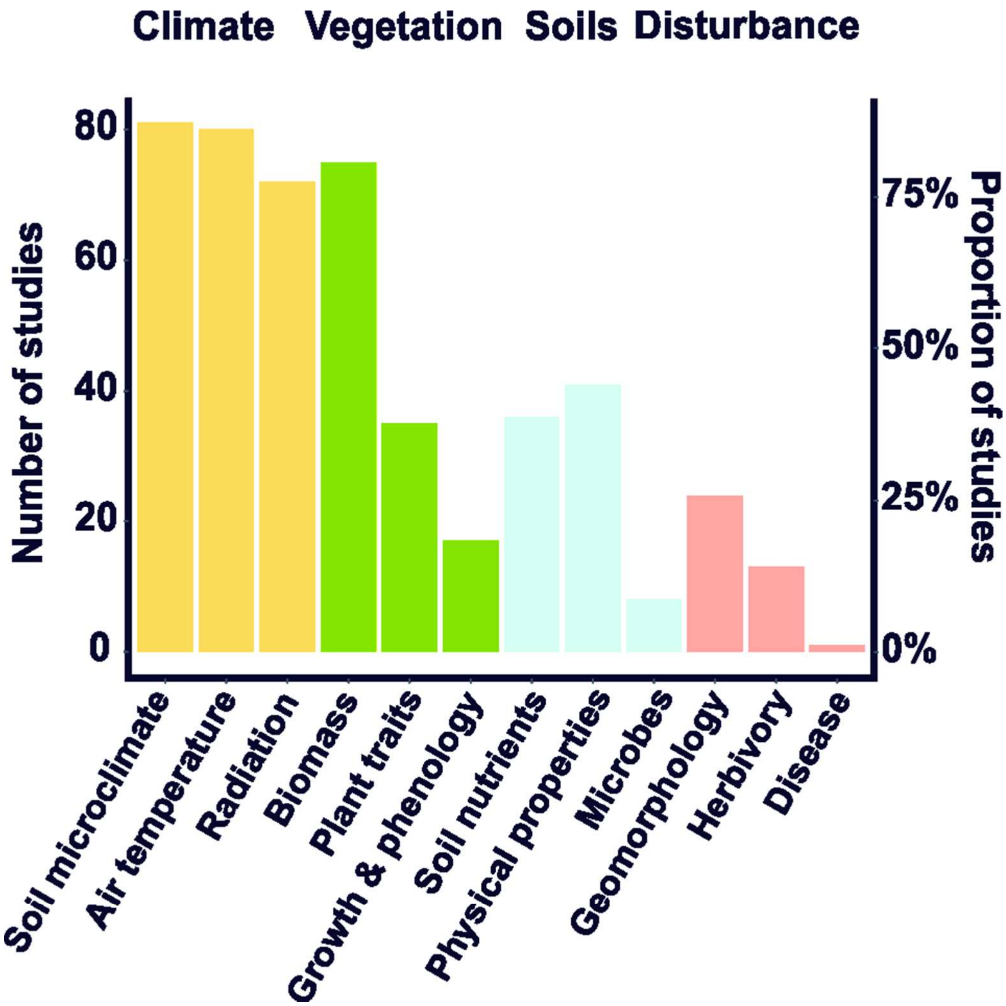

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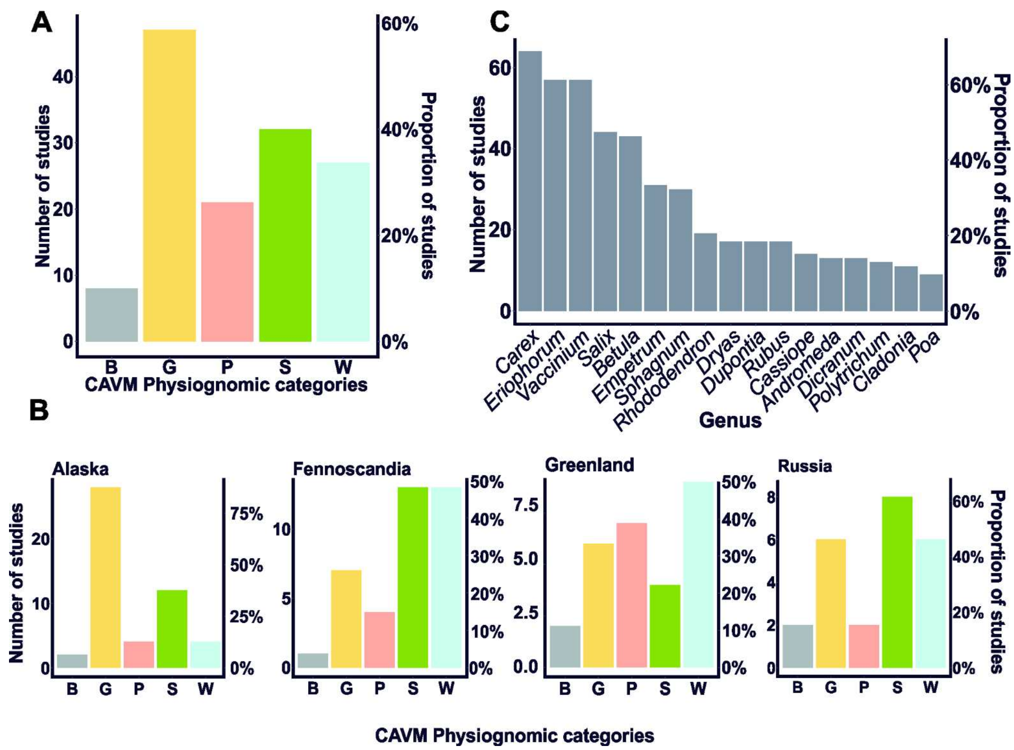

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Table 1. Environmental categories and classes used to explain CO_2 fluxes. Leaf area index (LAI) measures the amount of leaf area in a canopy per unit ground area (m^2 m^2; Asner et al., 2003). The normalized difference vegetation index (NDVI) or some other indices derived from remote sensing describe the amount of green biomass and/or LAI. Number in parentheses indicate the number of studies (0-93) to include the environmental categories/classes.

Categories	**Climate (91)**	**Vegetation (79)**	**Soils (54)**	**Disturbance (38)**
Classes	Air temperature (80) Radiation (72) -Photosynthetically active radiation (PAR)	Biomass (75) -cover, biomass, LAI -remotely sensed parameters (NDVI) Plant traits (35) -leaf N -leaf cover/area	Soil nutrients (36) -C, N, P, -pH -litter biomass Physical properties (41) -soil type, texture	Geomorphology (24) -permafrost thaw, cryoturbation, fluvial processes Herbivory (13) -small & large mammals

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	Soil microclimate (81) -topsoil temperature -active layer depth -moisture -water table height	-vegetation height Growth & phenology (17) -shoot, root, leaf, biomass growth -phenology	-organic layer depth Microbes (8) -microbial biomass, activity, community structure	-birds -insect outbreaks Disease (1) -plant pathogens

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Category	Knowledge level	Future research needs	Mechanisms	Importance
Fluxes	Good	Combination of soil respiration and NEE. Linkages to other greenhouse gas fluxes. Upscaling of fluxes.	Soil respiration & ER define NEE in a changing climate and disturbance regime. The role of other gas fluxes in global change. More detailed information on spatio-temporal variation and hot spots.	Urgent
Climate	Very good	Temperature extremes. Growing-season length.	Climate warming and changes in precipitation. Changes in dynamics.	Less urgent
Vegetation	Good	Barren and low-shrubs. Cryptograms.	Shrubification, vegetation shift. The role of mosses.	Moderate
Soils	Poor	Soil nutrients, SOC stocks and fluxes. Microbial biomass, community and activity.	Substrate quality important for GPP, regulates temperature sensitivity of ER. Changes in SOC stocks. Microbial effects and response to global warming.	Urgent
Disturbance	Poor	Geomorphology, permafrost dynamics, fire, disease.	Potential changes in geomorphological processes. Increase of fire and disease outbreaks. More CO_2 losses to the	Urgent

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		Herbivory.	atmosphere. Herbivory effects of different species in various environments.	

Table 2. Chamber-derived CO_2 fluxes and environmental categories studied, their knowledge level, research gaps, and importance of the topics in the global change - context.

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Appendix

Supplementary Material 1. Articles in the review.

Arens SJT, Sullivan PF and Welker JM (2008) Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem. *Journal of Geophysical Research-Biogeosciences* 113(G3): 10.

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Bokhorst S, Bjerke JW, Street LE, et al. (2011) Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO2 flux responses. *Global Change Biology* 17(9): 2817–2830.

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Brummell ME, Farrell RE and Siciliano SD (2012) Greenhouse gas soil production and surface fluxes at a high arctic polar oasis. *Soil Biology and Biochemistry* 52: 1–12.

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Supplementary Material 2. Methods in the systematic review

1. Data collection

This article is based on a literature review of chamber-derived CO_2 flux studies during the growing season in the Arctic tundra. The survey was conducted via ISI Web of Science (WoS) for articles published in the years 2000-2016. The search was carried out using a query that accounted for the region, scale, flux terminology, and different vegetation types: (tundra or arctic) and ecosystem and (“CO2 flux” or “carbon dioxide emissions” or “greenhouse gas exchange” or “CO2 exchange” or “carbon exchange” or “carbon flux”) and (meadow or sedge or tussock or hummock or heath or herb or grass or grassland or graminoid or forb or moss or bryophyte or lichen or "cushion plant" or shrub or tree). The query resulted in 242 articles out of which we included approximately 20 % of the studies. Firstly, we wanted to focus on soil chamber measurements and, therefore, excluded studies with eddy covariance or leaf cuvette measurements only. Secondly, only studies that included growing season measurements were taken into account. Studies with GPP, ER, and/or NEE measurements were included. Boreal regions were excluded from the review as we wanted to focus on tundra patterns and processes only, although they are usually included in the carbon balance assessments of Arctic regions (Belshe et al., 2013; McGuire et al., 2010; Treat et al., 2015). However, we included studies with sub-Arctic and Arctic peatlands and fens due to their importance in tundra carbon cycling. Additional articles were derived from the references of the selected publications.

The final 93 publications were read through systematically in order to collect data on the 1) measurement information, 2) study design and location, and 3) environmental variables used to explain the CO_2 fluxes. All the environmental variables measured and described were taken into account, also derived from the study design descriptions (e.g. organic layer depth). The variables were further divided into the following categories and their classes: climate (air temperature, photosynthetically active radiation, soil temperature, soil moisture), vegetation (biomass, plant traits, growth & phenology), soils (physical, chemical and biological) and disturbance (geomorphology, herbivory, disease). To our knowledge, at least seven articles were partly using the same CO_2 flux data, but the other environmental variables used in these studies was variable.

Information on the dominant and secondary species was also collected, and the vegetation data was further classified into Circumpolar Arctic Vegetation Map (CAVM) physiognomic units (Walker et al., 2005). CAVM was developed for landscape-scale analysis and does not consider fine-scale variation but we wanted to classify the vegetation data according to a widely-used vegetation classification. Furthermore, we recognize that classification was sometimes subjective and based on limited data on the species cover. Principally, we defined plots that were described to have only limited vegetation cover, or were described

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as barren or polar desert, to physiognomic unit B; plots that had tussocks and were mainly dominated by *Eriophorum, Carex,* and mosses to unit G; plots with a dominance of *Dryas*, *Cassiope,* and other prostrate-dwarf shrubs, such as *Salix arctica* and *S. polaris,* to unit P; erect-shrubs such as *Betula nana, Salix glauca, Rhododendron tomentosum, Vaccinium vitis-idaea* to unit S; and, plots described to be on wetland (bog, fen) to unit W.

2. Other data sets used in the figures

The data for Figure 4 was acquired from WorldClim 1970-2000 (average temperature and yearly cumulative precipitation at 2.5 minutes resolution; Fick & Hijmans, 2017), Soilgrid (topsoil pH at approx. 1 km resolution; Hengl et al., 2017), NCSCDv2 (soil organic carbon content at approx. 10 km resolution; Hugelius et al., 2013), TERRA/MODIS NDVI-product (from 1st of July, 2015 at approx. 10 km resolution; NASA, 2017) and GTOPO DEM (elevation at approx. 1 km resolution; USGS, 2004). The data was processed with the *raster* package (Hijmans et al. 2016) in R program. The values from the circumpolar data sets were extracted to the observation points. Raster extent varied and, therefore, 10-25 observation sites did not receive any values given they were outside the extent (e.g. soil pH map in southern Svalbard). The tundra area for describing the entire Arctic variation was defined by Ecoregions (Dinerstein et al., 2017). The entire Arctic variation data was rescaled to 10 km resolution for the plots.

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Supplementary Material 3. Table with 20 most cited publications. Citations were derived from Web of Science, 16th of March 2017. Fluxes describe the CO_2 fluxes measured in the study (SR= soil respiration), manipulation defines whether the study is based on manipulative observations (e.g. experimental warming) and region defines study location(s) of the observations.

Authors	Year	Title	Journal	Citations	Fluxes	Manipulation	Region
Schuur et al.	2009	The effect of permafrost thaw on old carbon release and net carbon exchange from tundra	NATURE	423	GPP, ER, NEE	0	Alaska
Welker et al.	2000	Annual CO2 flux in dry and moist arctic tundra: Field responses to increases in summer temperatures and winter snow depth	CLIMATIC CHANGE	131	NEE	1	Alaska
Oberbauer et al.	2007	Tundra CO2 fluxes in response to experimental warming across latitudinal and moisture gradients	ECOLOGICAL MONOGRAPHS	124	GPP, ER, NEE	1	Canada
Welker et al.	2004	CO2 exchange in three Canadian High Arctic ecosystems: response to long-term experimental warming	GLOBAL CHANGE BIOLOGY	117	GPP, ER, NEE	1	Canada
Kutzbach et al.	2007	CO2 flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression	BIOGEOSCIENCES	109	NEE	0	Fennoscandia, Russia
Christensen et al.	2000	Trace gas exchange in a high-arctic valley 1. Variations in CO2 and CH4 flux between tundra vegetation types	GLOBAL BIOGEOCHEMICAL CYCL	107	GPP, ER, NEE	0	Greenland
Johansson et al.	2006	Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing	GLOBAL CHANGE BIOLOGY	106	NEE	1	Fennoscandia
Boelman et al.	2003	Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra	OECOLOGIA	104	GPP, ER, NEE	1	Alaska
Shaver et al.	2007	Functional convergence in regulation of net CO2 flux in heterogeneous tundra landscapes in Alaska and Sweden	JOURNAL OF ECOLOGY	92	GPP, ER, NEE	0	Fennoscandia
Street et al.	2007	What is the relationship between changes in canopy leaf area and changes in photosynthetic CO2 flux in arctic ecosystems?	JOURNAL OF ECOLOGY	87	GPP	0	Fennoscandia, Alaska
Johnson et al.	2000	Plant carbon-nutrient interactions control CO2 exchange in Alaskan wet sedge tundra ecosystems	ECOLOGY	81	GPP, ER, NEE, SR	1	Alaska
Heikkinen et al.	2004	Carbon balance in East European tundra	GLOBAL BIOGEOCHEMICAL CYCL	59	GPP, ER, NEE, SR	0	Russia
Biasi et al.	2008	Initial effects of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia	PLANT AND SOIL	59	GPP, ER, NEE	1	Siberia
Bokhorst et al.	2011	Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO2 flux responses	GLOBAL CHANGE BIOLOGY	56	GPP, ER, NEE, SR	1	Fennoscandia
Sullivan et al.	2008	Temperature and microtopography interact to control carbon cycling in a high arctic fen	ECOSYSTEMS	54	GPP, ER, NEE	1	Greenland
Grogan & Jonasson	2005	Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types	GLOBAL CHANGE BIOLOGY	54	ER	1	Fennoscandia
Grogan & Chapin	2000	Initial effects of experimental warming on above- and belowground components of net ecosystem CO2 exchange in arctic tundra	OECOLOGIA	54	GPP, ER, NEE, SR	1	Alaska
Natali et al.	2011	Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra	GLOBAL CHANGE BIOLOGY	53	GPP, ER, NEE, SR	1	Alaska
Bäckstrand et al.	2010	Annual carbon gas budget for a subarctic peatland, Northern Sweden	BIOGEOSCIENCES	51	NEE	0	Fennoscandia
Larsen et al.	2007	Significance of cold-season respiration and photosynthesis in a subarctic heath ecosystem in Northern Sweden	GLOBAL CHANGE BIOLOGY	47	GPP, ER, NEE	1	Fennoscandia

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Supplementary Material 4. Descriptive data from the 93 articles included in this review. The different columns indicate studies with GPP, ER, and/or NEE measurements, and an average of all CO_2 flux studies. The row names are different classifications of the data which describe information of the studies, study designs, methods, measurements, vegetation, and climatological, soil, and disturbance variables. Cells indicate the number of the studies (except for average number of citations). In the spatial study designs, the focus is on understanding the CO_2 fluxes in the landscape (related to e.g. different vegetation types or topographic positions) whereas in the temporal study designs, the focus is to understand CO_2 dynamics. In manipulative studies, environmental conditions have been modified. In some cases, no data was available (e.g. chamber size).

Studies with measurements of		**GPP**	**ER**	**NEE**	**All fluxes**
General information		**Number of**	**studies with**	**observations**	**of**
Arctic	Arctic	28	29	29	32
	Oroarctic	31	33	36	39
	High Arctic	27	30	29	33
Region	Alaska	26	29	27	32
	Canada	7	7	7	8
	Fennoscandia	20	22	24	27
	Russia	12	12	13	13
	Greenland	16	15	17	18
	Svalbard	5	7	7	8
Publication year	2010-2016	32	36	34	39
	2005-2010	19	19	20	23
	2000-2005	9	9	9	9
Average number of citations		35	34	37	36
Study designs					
Spatial/temporal	Spatial	21	22	24	25
	Temporal	18	20	19	21
	Spatial and temporal	31	34	33	39

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Observational/manipulative	Observational	42	46	47	53
	Manipulative	35	37	36	39
	Warming	20	20	21	21
	Nutrient addition	7	6	6	7
	Water modifications	5	5	5	5
Median number of observations	All	24	24	29	26
	Spatial	40	40	41	42
	Temporal	18	18	18	18
	Spatial and temporal	18	19	18	20
	Manipulative	20	20	20	20
	Observational	30	29	26	29
Median number of sites	All	3	3	3	3
	Observational	4	4	4	4
Study methods					
Chamber types	Manual	70	75	73	82
	Automatic	8	9	11	11
Chamber size	Edges/diameter< 25 cm	39	43	42	46
	Edges/diameter 25-50 cm	22	24	23	26
	Edges/diameter >50 cm	17	17	19	21
	Height <25 cm	45	49	46	52
	Height 25-50 cm	17	20	21	23
	Height > 50 cm	9	9	9	9
Chamber type	LI-COR	48	53	51	59
	EGM	15	15	15	16
	Vaisala	2	2	2	2

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CO_2 measurements					
Fluxes	GPP	78	76	74	78
	ER	76	84	77	84
	NEE	74	77	84	84
	Soil respiration	12	14	14	15
Temporal measurements	Summer season (J-A)	58	63	62	69
	Cold-season (A, M, S, O)	14	18	20	21
	Winter	16	17	18	19
	Yearly	29	33	33	35
Other flux measurements	Eddy covariance	9	10	11	11
	Leaf cuvette	4	5	4	5
Other gas fluxes	N_2O	2	2	2	3
	CH_4	20	21	23	24
Vegetation					
Peatland		21	22	23	23
Vegetation cover	Species/PFT/Total cover	44	44	44	44
Biomass	Aboveground species/PFT/Total	44	43	43	44
	Belowground biomass	10	12	12	12
	LAI	21	21	20	23
	NDVI	27	27	26	29
	(field or satellite-based)				
Any biomass (cover + biomass)		75	75	75	75
Plant traits	Leaf chemical properties	15	15	15	17

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	Leaf cover	11	12	12	13
	Vegetation height	9	10	10	11
Growth & phenology		17	17	17	17
Climate					
Surface	Air temperature	74	77	78	80
	PAR	69	70	71	72
Soils	Soil temperature	64	69	66	74
	Thaw depth	37	41	42	45
	Soil moisture	39	42	39	46
	Water table height	32	33	34	35
Soils					
Nutrients	C	15	15	15	15
	N	18	18	18	18
	P	5	5	5	5
	pH	13	13	13	15
	Litter biomass	6	6	5	7
Physical	Organic layer depth	25	28	25	28
	Soil type	13	14	13	15
	Texture	25	25	25	27
Microbes	Microbial community	1	1	1	1
	Microbial biomass	4	5	4	5
	Microbial activity	4	4	3	4
Disturbance					
Geomorphology	Permafrost	10	11	12	12
	Cryoturbation	6	8	7	8
	Fluvial activity	4	4	4	4

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	Hummocks & hollows	9	10	10	10
Herbivory	Reindeer	4	5	5	5
	Muskoxen	3	3	3	3
	Small mammals	1	1	1	1
	Goose	4	4	4	4

Supplementary Material 5. Dominant species as informed by the authors. From vegetation informed only at genera-level, *Carex* (30 studies), *Sphagnum* (19 studies), *Eriophorum* (12 studies), and *Salix* (7 studies), were studied the most.

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Species	**Functional group**	**Number of studies**
Betula nana	Deciduous shrub	29
Empetrum hermaphroditum/nigrum	Evergreen shrub	24
Eriophorum vaginatum	Graminoid	23
Vaccinium uliginosum	Deciduous shrub	19
Vaccinium vitis-idaea	Deciduous shrub	17
Eriophorum angustifolium	Graminoid	15
Cassiope tetragona	Evergreen shrub	11
Rubus chamaemorus	Forb	11
Eriophorum scheuchzeri	Graminoid	10
Carex aquatilis	Graminoid	9
Dryas octopetala	Evergreen shrub	9
Carex stans	Graminoid	8
Rhododendron tomentosum	Evergreen shrub	8
Salix arctica	Deciduous shrub	8
Salix glauca	Deciduous shrub	8
Salix pulchra	Deciduous shrub	8
Rhododendron subarcticum	Evergreen	7

	shrub	
Andromeda polifolia	Evergreen shrub	6
Dryas integrifolia	Evergreen shrub	6
Dupontia psilosantha	Graminoid	6
Salix polaris	Deciduous shrub	6

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